

AN ANALYSIS BY SELECTION AND CROSSING OF
GENETIC FACTORS INVOLVED IN DEFECTIVE
VENATION, A VARIABLE CHARACTER
OF THE PARASITIC WASP,
HABROBRACON JUGLANDIS (ASHMEAD)



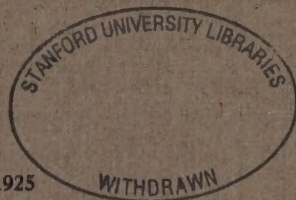
BY
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AN ANALYSIS BY SELECTION AND CROSSING, OF GENETIC FACTORS INVOLVED IN DEFECTIVE VENATION, A VARIABLE CHARACTER OF THE PARASITIC WASP, *HABROBRACON* *JUGLANDIS* (ASHMEAD)

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INTRODUCTION

This insect was first used for genetic research by P. W. WHITING in 1919, and it has been bred extensively in his laboratory since that time. A large amount of data has been gathered dealing with the behavior of several mutant genes, chief among which are orange eye and defective venation (WHITING 1921 a, b, 1924). Several stocks of the wasp show a vein defect consisting of partial or complete absence of the fourth branch of the radius. The origin of this defect and its variations are described by WHITING (1924). The progeny of a female possessing a factor for this defect range

from normal to complete absence of vein. The amount of defect in any individual is estimated and placed in one of nine arbitrary grades. In the tabulations 0 signifies the normal type, or no defect. The number 1 represents the absence of one-fourth of the vein in one wing, 2 the absence of one-half of it in one wing or one-fourth of it in both wings, and so on, 8 meaning the complete absence of both veins. The defect is not symmetrically disposed. All the progeny of a mating, or series of matings, are graded and the mean is taken. This mean may be that of the total number of wasps, including type individuals (Mn); or it may be that of the defectives only (Md). The percentage of defectives (percent d) is usually added. It is found that at a given temperature the Mn, Md and percent d are fairly constant within a pure stock. The main portion of the present experiments has to do with an investigation of the behavior of these constants under selection and crossing.

STOCK 3

This stock, called the Orange High-defective stock, was isolated in December, 1920, by WHITING. During the year 1901 it gave the following averages (WHITING 1924, p. 28):

	<i>Percent d</i>	<i>Md</i>
Males.....	95.2	6.61
Females.....	85.8	5.84

Cultures made in 1922 averaged higher:

	<i>Percent d</i>	<i>Md</i>
Males.....	95.8	6.97
Females.....	92.7	6.39

WHITING thinks that "it is probable, therefore, that a change in the direction of increased defectiveness has occurred without conscious selection." The early cultures of the present experiment gave (839 wasps):

	<i>Percent d</i>	<i>Md</i>
Males.....	99.4	6.47
Females.....	95.1	5.98

The percentages are higher than in the previous year, but the means of the defectives are lower. Possibly this discrepancy is due to a difference in estimating extremely low-defective specimens. If the investigator is inclined to call an insect with only a faint indication of defect a type specimen, the percentage will be lowered and the average raised. WHITING (1922, table J) gives only 0.22 percent for males of grade 1, while the wasps bred in 1923 show 1.19 percent defective males in this grade. Further allowance must be made for differences in cultural conditions when

experiments are conducted under different circumstances. In a word, the above data, while suggestive, are not sufficiently critical to demonstrate that there has been a change in the stock since 1922.

Selection within stock 3

The purpose of the first of the present series of experiments was to determine whether a change in the average or in the percentage of defectives can be induced by selection. Accordingly, two lines of cultures were conducted under identical conditions of temperature and food supply; in line A matings were made between wasps of low defect, whenever possible from type specimens; in line B the selection was for high defect, and this meant that in nearly all cases crosses were made between two completely defective individuals (grade 8). Line A was carried through nineteen generations; line B through twenty-two generations. These cultures were begun in the fall of 1922 at exactly 30° C; but it was found that at this temperature the number of low-grade defectives in line A was so small that it was difficult to get enough of them to make reasonable progress; for this reason the temperature was lowered two degrees the following spring and kept there, with some unintentional minor variations, until December, 1923, after which it was again raised to 30 degrees. This change of temperature complicates the interpretation of the data, since it is necessary to compare the wasps of the two lines that were bred simultaneously, rather than those of the comparable successive generations in each line. The tables and graphs show what effect the two-degree drop had on all wasps.

Data

Table 1 summarizes the nineteen generations of cultures in line A. The numbers of the first six generations were not large enough to justify separate summaries, and they have been grouped in such a way that group 2 comprises the second and third generations, and group 3 the fourth, fifth, and sixth generations. Groups 4 to 16 correspond to generations 7 to 19. Table 2 summarizes the wasps of line B that were bred simultaneously with each of the sixteen groups in table 1, irrespective of the generations they represent.

A study of these tables, as well as an examination of the data of previous work (WHITING 1924) shows that the number of males obtained is generally in excess of the number of females; also, that the average of defect is higher in the males than in the females. The first of these two facts is accounted for when we remember that males are produced from unfertilized eggs; if the male of any particular mating happens to be sterile, or

TABLE 1

Showing that continued breeding from stock-3 wasps selected for low defect produced no significant change in the average of defect or percentage of defectives.

GROUP	SEX	GRADE OF DEFECT										TOTAL	MEAN DEFECT	PERCENT DEFEC- TIVE
		0	1	2	3	4	5	6	7	8				
1.....	♂♂	1	2	3	0	11	6	15	18	22	78	6.07±.15	98.72	
	♀♀	7	2	3	2	9	8	12	12	11	66	5.05±.21	89.40	
2.....	♂♂	1	1	3	4	6	5	15	17	40	92	6.50±.13	98.92	
	♀♀	1	2	6	3	21	7	25	27	32	124	5.94±.11	99.20	
3.....	♂♂	3	1	4	2	16	7	10	14	35	92	6.00±.15	96.74	
	♀♀	7	1	7	8	20	4	14	16	23	100	5.19±.14	93.00	
4.....	♂♂	9	9	10	13	39	26	51	55	65	277	5.65±.08	96.75	
	♀♀	13	10	11	9	33	34	46	46	23	225	5.08±.10	94.89	
5.....	♂♂	1	1	3	2	5	3	12	10	19	56	6.10±.18	98.20	
	♀♀	6	6	3	6	8	6	9	8	8	60	4.43±.23	90.00	
6.....	♂♂	14	14	12	10	31	17	39	43	54	234	5.27±.11	94.00	
	♀♀	2	0	1	4	2	4	0	7	3	23	5.00±.34	91.30	
7.....	♂♂	1	3	0	3	9	7	14	19	13	69	5.85±.15	98.55	
	♀♀	1	1	3	1	4	14	29	23	10	86	5.94±.11	98.84	
8.....	♂♂	27	17	11	18	42	36	70	72	56	349	5.19±.09	92.27	
	♀♀	13	3	12	11	25	37	55	36	17	209	5.08±.10	93.78	
9.....	♂♂	13	9	15	20	49	39	78	93	36	352	5.39±.07	96.31	
	♀♀	9	2	3	8	11	8	34	18	4	97	4.92±.15	98.72	
10.....	♂♂	10	2	6	8	19	16	50	50	17	178	5.50±.10	94.39	
	♀♀	10	3	5	7	18	19	51	20	11	144	5.10±.12	93.00	
11.....	♂♂	26	15	29	20	43	32	75	47	27	314	4.65±.09	91.72	
	♀♀	15	3	10	18	31	13	66	37	9	202	4.91±.09	92.58	
12.....	♂♂	23	6	11	9	17	20	60	49	38	233	5.28±.12	90.13	
	♀♀	1	2	4	2	8	8	32	13	12	82	5.70±.11	98.78	
13.....	♂♂	3	2	7	4	14	9	56	54	60	209	6.33±.08	98.75	
	♀♀	8	3	6	6	13	16	59	37	26	174	5.67±.10	95.41	
14.....	♂♂	3	5	4	3	7	9	36	55	55	177	6.41±.09	98.30	
	♀♀	4	1	5	4	8	14	60	36	19	151	5.91±.09	97.36	

TABLE 1 (continued)

GROUP	SEX	GRADE OF DEFECT										TOTAL	MEAN DEFECT	PERCENT DEFECTIVE
		0	1	2	3	4	5	6	7	8				
15.....	♂♂	1	1	2	0	4	3	12	13	26	87	6.87±.11	98.85	
	♀♀	5	0	7	0	2	2	10	10	5	41	5.00±.28	87.80	
16.....	♂♂	1	2	5	5	5	4	15	13	15	65	5.66±.18	98.47	
	♀♀	2	2	3	2	4	5	17	6	5	46	5.20±.21	95.66	
All grades	♂♂	137	90	125	121	317	239	608	647	578	2862	5.58±.03	95.28	
	♀♀	104	41	89	91	217	199	519	352	218	1830	5.28±.03	94.27	

TABLE 2

Showing that continued breeding from stock-3 wasps selected for high defect produced no significant change in mean defect or percentage of defectives.

GROUP	SEX	GRADE OF DEFECT										TOTAL	MEAN DEFECT	PERCENT DEFECTIVES
		0	1	2	3	4	5	6	7	8				
1	♂♂	2	1	1	1	4	2	16	22	32	81	6.64±.12	97.53	
	♀♀	4	0	7	2	6	11	13	20	21	84	5.77±.16	95.12	
2	♂♂	3	1	2	4	21	12	37	61	120	261	6.75±.07	98.86	
	♀♀	10	6	7	7	16	15	36	54	57	208	5.91±.11	95.20	
3	♂♂	1	0	1	1	3	2	13	15	31	67	6.86±.13	98.51	
	♀♀	5	1	5	2	15	3	16	22	28	97	5.83±.16	94.85	
4	♂♂	8	9	9	13	38	31	75	83	113	379	6.09±.02	97.89	
	♀♀	4	3	8	7	26	13	60	54	54	229	6.02±.08	98.26	
5	♂♂	0	0	6	2	19	9	26	27	31	120	6.10±.11	100.00	
	♀♀	4	3	3	5	17	16	16	16	9	89	5.08±.15	95.50	
6	♂♂	6	5	6	8	6	7	24	31	29	122	5.63±.15	95.08	
	♀♀	6	1	2	2	5	6	8	4	4	38	4.44±.28	84.21	
7	♂♂	4	9	11	9	29	29	53	80	63	287	5.95±.08	98.61	
	♀♀	12	3	6	7	7	17	38	39	17	146	5.38±.13	91.78	
8	♂♂	10	3	13	15	43	33	52	42	19	230	5.22±.09	96.07	
	♀♀	10	2	15	17	20	30	42	39	8	183	4.93±.10	94.54	
9	♂♂	13	9	30	28	53	63	160	93	42	491	5.35±.06	97.36	
	♀♀	11	3	13	15	37	34	110	74	42	339	5.62±.07	96.76	
10	♂♂	2	3	10	5	27	15	40	46	28	176	5.72±.09	98.87	
	♀♀	10	6	12	10	28	29	73	42	16	226	5.20±.09	95.58	

TABLE 2 (continued)

GROUP	SEX	GRADE OF DEFECT										TOTAL	MEAN DFFECT	PERCENT DEFECT- TIVE
		0	1	2	3	4	5	6	7	8				
11	♂♂	8	7	18	14	29	37	95	59	23	290	5.35±.08	97.24	
	♀♀	14	9	16	15	36	37	82	40	22	271	5.03±.09	94.84	
12	♂♂	11	7	15	12	26	21	69	100	72	333	5.92±.07	96.70	
	♀♀	5	2	5	5	12	18	43	44	37	171	6.00±.16	97.08	
13	♂♂	8	4	15	6	12	20	47	88	78	278	6.19±.08	97.12	
	♀♀	8	3	11	9	16	30	81	76	42	276	5.87±.08	97.10	
14	♂♂	7	5	9	10	17	24	81	151	171	475	6.63±.05	98.53	
	♀♀	5	3	6	7	7	28	97	87	48	288	6.17±.06	98.27	
15	♂♂	5	1	5	7	9	15	48	84	98	272	6.62±.07	98.16	
	♀♀	12	9	7	10	10	15	58	62	28	211	5.56±.10	94.30	
16	♂♂	4	0	3	7	4	6	17	44	20	105	6.12±.13	96.19	
	♀♀	6	3	5	7	13	10	42	35	20	141	5.62±.12	95.75	
Odd culture	♂♂	6	2	4	0	9	3	18	40	95	145			
	♀♀	10	6	7	6	17	12	24	25	30	137			
All grades	♂♂	98	66	158	142	348	329	871	1066	1045	4122	6.03±.02	97.47	
	♀♀	136	63	135	133	288	324	839	733	483	3134	5.59±.03	95.66	
												5.81	96.57	

if the mating for any reason is unsuccessful, the offspring will be all males. The second fact, the higher average defect of the males, is probably correlated with their haploid character, inasmuch as in females the normal allelomorph for some of the defect factors may be present. These two facts taken together make it necessary, if successive groups are to be compared, to compute the average of each sex separately; otherwise those cultures in which the males predominate will show a higher average than those in which the sexes are approximately equal.

Diagram 1 shows the distribution of the amount of defect. The mode for females is at grade 6, for males at 7. The minor modes at grades 2 and 4 may be due to causes operative in development (POTTER, unpublished), but their significance is not clear. The females show a smaller percentage of wasps in the high grades and a larger percentage in the low grades than the males. The distribution for lines A and B is very similar.

Diagram 2 shows how the sixteen groups of line A compare with those of line B as to average of defect and percentage of defectives. The mean of

both lines dropped when the temperature was lowered, and minor fluctuations are, in the main, parallel. Line A is, in general, lower than line B; the exceptions in percentages are probably not significant, and the lower grades of defect of line B in groups 6, 7, and 8 may possibly be accounted for by the small number of females or accidental excess of type individuals. The conspicuous ups and downs are doubtless due to accidental lapses in incubator efficiency or to changes in food supply. The significant thing is that the two lines rise and fall together, indicating that the variations are environmental rather than genetic.

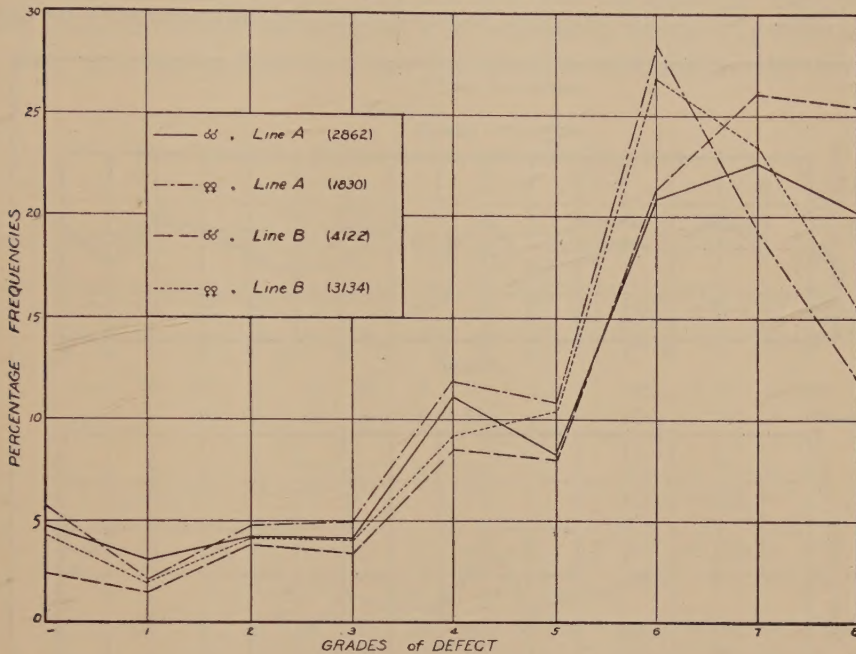


DIAGRAM 1.—The percentage of wasps (ordinates) in each grade of defect (abscissae) in four lines of stock 3. Line A was selected for low defect, line B for high defect.

At times the progenies of individual cultures through two or three generations gave promise of yielding to selection. The best example of this was No. 836 in the fourteenth generation of line B. It maintained an Mn of 6.40 and a percent d of 98.75 through four generations; but the later offspring fell lower, and the mean of about a thousand descendants of this culture was 6.25, the last ones being still lower.

Conclusions

A careful study of the data of this experiment justifies the conclusion that selection through twenty-two generations has had no effect on stock 3,

for the difference between lines A and B is not increased as selection proceeds. The probable error indicates that the difference between any two of the groups is not significant; however, one cannot disregard the persistence of this difference in thirteen of the sixteen groups; moreover, the difference between the totals of the two lines for the Mn is $.45 \pm .034$ percent for males, and $.31 \pm .042$ percent for females. This difference is evidently significant and an explanation is necessary. It is possible that the first few generations did show the effect of selection through the segregation of a modifying factor, or a mutation may have occurred in one of the lines. The writer suspects, however, that the difference may be due,

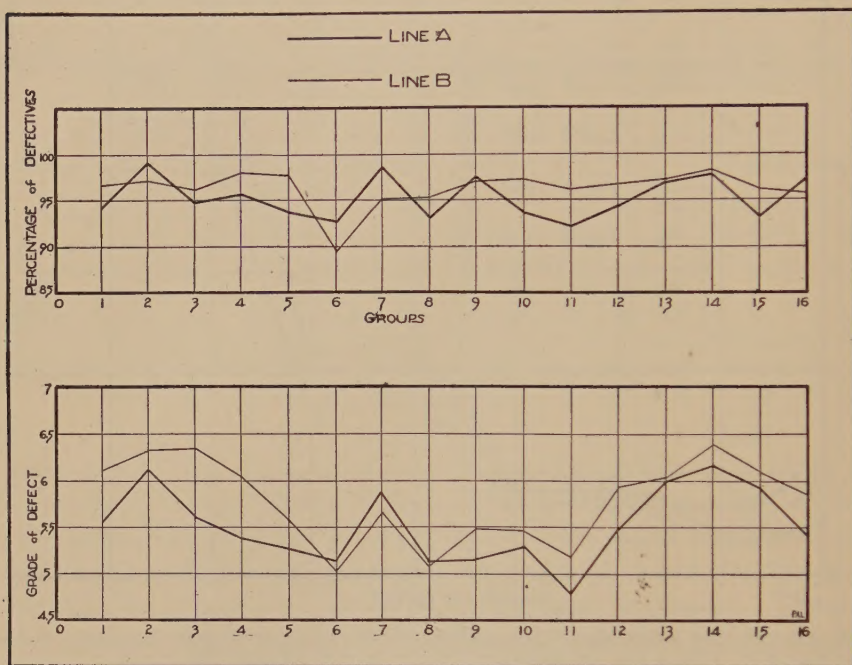


DIAGRAM 2.—Percentage of defectives and of mean defect (ordinates) in the successive groups (abscissae) of lines A and B, stock 3.

in part at least, to an entirely different cause. When examining the wasps it is often difficult to decide whether to put an individual in, say, group 5 or group 6. The decision must be made without accurate measurement, and subconsciously one prefers 5 to 6 in line A and *vice versa* in line B. Such inaccuracy, even if only occasional, may affect the results preceptibly. At any rate, in view of such a possibility, it is thought safer not to attach too much significance to the constant difference between lines A and B.

STOCK 14

When stock 14 was first bred from in October, 1923, there was no intention of performing a selection experiment. The stock, which is black-eyed and of mixed origin, was known to contain one or more factors for defect different from that of stock 3; and it was thought that by proper crossing and selection from the cross, a strain might be obtained containing both sets of factors. In keeping up this stock, only individuals of high defect were bred, and it soon became evident that a change of considerable magnitude was taking place. The selection was not rigid, no attempt being made to control the matings; a high-defective female was selected for each new culture, but as a rule no attention was paid to the male

TABLE 3

Showing the effect produced by selective breeding in stock 14.

GROUP	SEX	GRADE OF DEFECT										TOTAL	MEAN DEFECT	PERCENT DEFECTIVE
		0	1	2	3	4	5	6	7	8				
1 and 2...	♂♂	60	20	25	9	18	10	9	1	4	156	2.00±.12	61.54	
	♀♀	58	19	10	14	16	3	4	3	0	127	1.61±.12	54.38	
3.....	♂♂	90	42	42	22	28	8	10	5	1	248	1.80±.08	63.72	
	♀♀	59	20	33	22	24	10	16	4	0	188	2.24±.09	68.62	
4.....	♂♂	89	16	26	23	23	12	22	12	2	225	2.32±.07	60.45	
	♀♀	53	8	8	19	15	7	15	2	0	127	2.20±.13	58.27	
5.....	♂♂	67	17	29	19	43	23	48	19	3	268	3.22±.10	75.00	
	♀♀	10	2	5	8	21	9	13	4	0	72	3.76±.16	86.12	
6.....	♂♂	118	24	54	36	44	26	64	35	15	416	3.11±.09	71.64	
	♀♀	51	14	31	20	32	20	35	12	4	219	3.10±.11	76.72	
7.....	♂♂	38	4	29	18	30	21	60	40	28	268	4.50±.11	85.82	
	♀♀	21	7	18	17	21	20	35	13	1	153	3.83±.12	86.28	
8.....	♂♂	30	8	18	13	14	14	33	23	29	182	4.40±.14	83.52	
	♀♀	25	6	19	17	15	13	19	13	3	130	3.45±.14	80.77	
9.....	♂♂	22	12	13	12	13	9	31	24	19	155	4.37±.15	85.81	
	♀♀	35	9	14	8	15	18	22	12	5	138	3.38±.17	74.64	
10.....	♂♂	3	1	4	0	1	2	5	5	12	33	5.57±.32	90.91	
	♀♀	5	1	0	1	1	4	1	2	9	24	5.00±.43	79.17	
No. 262	♂♂	16	9	11	9	7	10	38	47	38	185	5.39±.13	91.35	
	♀♀	14	8	10	12	11	18	22	21	15	131	4.55±.15	89.34	

involved. After ten generations of this kind of selective breeding the percentage of defectives had risen from 57.94 ± 1.9 to 85.04 ± 2.7 , and the average of defect (Mn) from $1.81 \pm .12$ to $5.29 \pm .43$. One strain in particular retained through four generations a percentage of 90.35 ± 1.9 and an average defect of $4.97 \pm .15$. The results of this part of the experiment are shown in table 3 and diagrams 3 and 4.

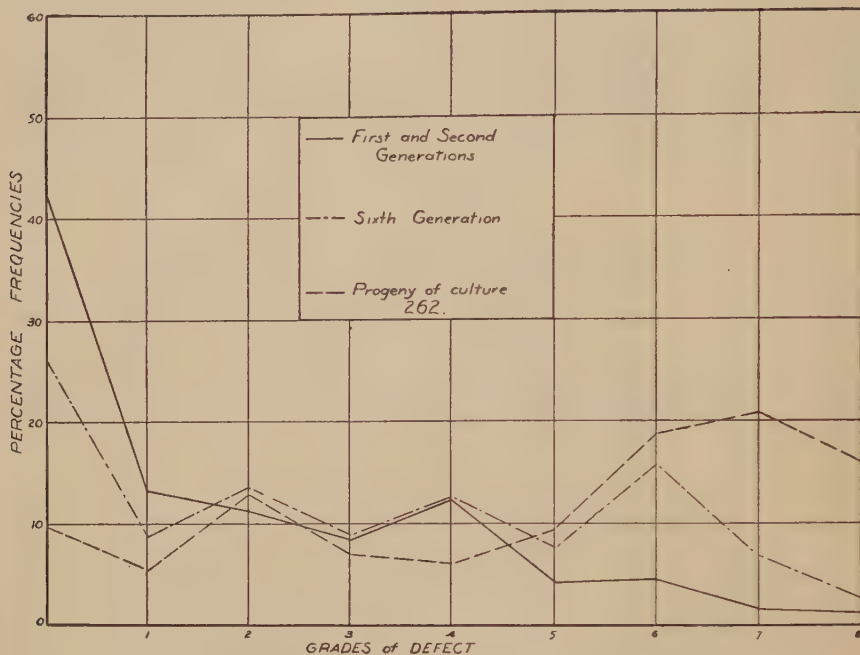


DIAGRAM 3.—Distribution of wasps with respect to grade of defect, in stock 14.

When seeking an explanation of the difference between this stock and stock 3 with reference to the results of selection, it may be observed that stock 3 was probably homozygous from the start, and that stock 14 had not yet been sufficiently inbred to eliminate heterozygosis of the various factors. It is desirable that more work be done to determine the limits beyond which selection will not be effective. If no such limit is reached, the conclusion would be justified that mutations of minor grade are occurring (ZELENY 1922).

BREEDING STOCK 3 TO STOCK 14

The method used

After twenty-two generations of selective inbreeding it was fairly well established that the defect in stock 3 is due to a single unit factor, or at

least to closely linked factors (EAST and JONES 1919). This gene is denoted by d and its allelomorph by D , though dominance is irregular (WHITING 1924, p. 12). Stock 14 evidently has one or more factors for defect that are independent of d ; for convenience these may be denoted by l , m , n . In order to bring all these factors together in one individual an experiment was decided upon which consists essentially in breeding wasps with d derived from stock 3 to stock 14. The fact that the female reproduces parthenogenetically and that the males thus produced are haploid, is a great aid in analyzing the effects of each cross. Of course, theoretically,

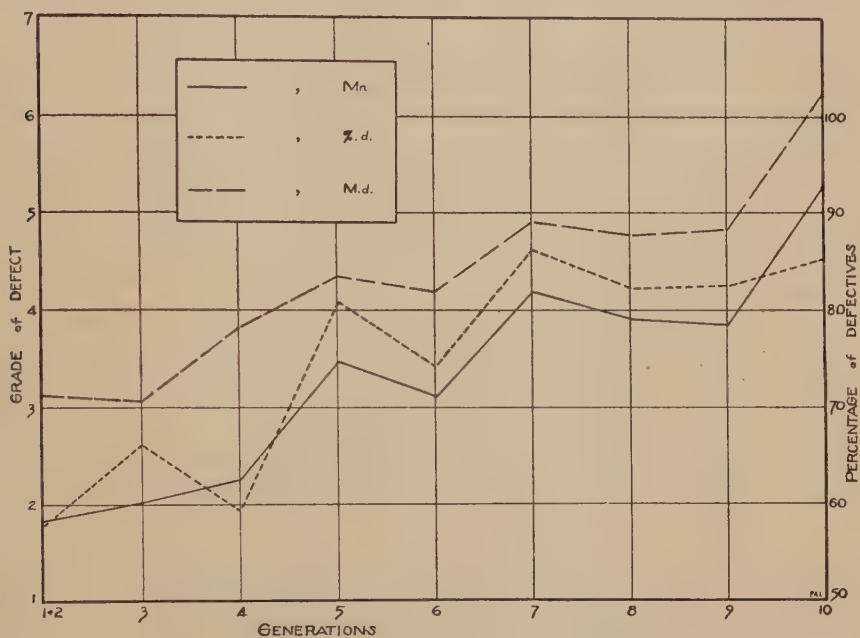
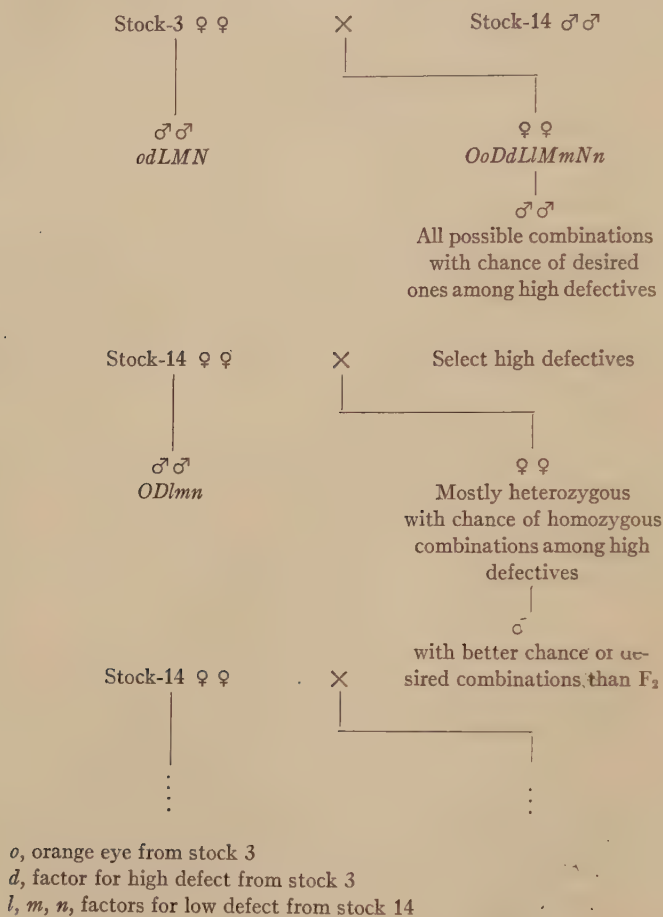


DIAGRAM 4.—Percentage of defectives and mean defect of successive generations of stock 14.

the combination desired could be obtained by haphazard selection from an ordinary F_2 generation; but since the phenotype gives no reliable clue to its genetic constitution, and since presumably several genes are involved, the chances of obtaining the right combination are very small, and many hundreds of individuals would have to be tested. For these reasons the following scheme was decided upon (WHITING 1923, 1924, p. 30). This means that the females of F_1 are bred parthenogenetically, and since the resulting males are haploid it is easy to make an analysis of the genetic constitution of the females used. From the males of F_2 a selection is made of individuals with high defect for further breeding,

this time with stock-14 females. If one uses four or five such males one may be reasonably certain that some of them possess the factor *d* and in addition one or more of the factors *l*, *m*, *n*. If the factor *d* should chance to be absent, the low averages resulting in the next generation would suffice to detect this fact. If all the factors *l*, *m*, *n*, are not present,—and the chance is that they are not,—there is hope of introducing them in the next cross with stock 14.



This scheme of upbreeding results in a sort of alternation of sexual with parthenogenetic generations; the odd numbers represent the sexually produced generations, the even numbers the offspring of virgin females. In the present experiment the process was carried through twelve generations before the final crosses were made.

Application of the method

Table 4 gives the general results of this experiment. The first cross was between females from stock 3, whose constitution was 5.18 as measured by the average Mn of the males they produced;¹ and males from stock 14, whose constitution was 1.81 as measured by their brothers. The resulting heterozygous females averaged 2.81, which number, however, should be raised if it is to be compared with the averages of the parents, because the females are regularly of lower grade than the males. There were no grade-8 individuals among these females, and those of grades 6 and 7 were not isolated in time to be used. Virgin females of grades 4 and 5 only were available for the next generation, but the offspring to be expected from these should not differ seriously from the progeny of grade-8 females (WHITING 1924, p. 40, 1a). Five of these medium-grade females were bred and produced 922 male offspring with an average defect of 3.30. From these, five high-defective orange males were selected and bred with high-defective females from stock 14. The latter stock had by this time shown the effects of selection; but a check on the defective status of the females used is available in their haploid male offspring; they carried an average defect (for males) of 2.61. The heterozygous female offspring averaged 3.52, which, though on a female basis is, nevertheless, slightly higher than that of the male averages of either parent. One of these females was grade-8 but was not obtained virgin, and five females of grade 6 and 7 were used for the fourth generation (second parthenogenetic). These females, whose sisters averaged 3.52, produced 608 males that averaged 4.49. The difference here is larger than it should be because the males are expected to be higher than the females.

This process was continued to the twelfth generation and all the essential data are included in table 4. Special considerations may be grouped under the three headings which follow.

Analyses

The stock-14 females used

These were on the average higher in each succeeding generation. The following summary of the male offspring of stock-14 females used in the

¹ There is, of course, a possibility that this average is affected by patrocliny. But if patrocliny were common enough to affect the average seriously we should expect it occasionally to affect eye color, whereas the 202 males examined from this cross were all orange. Moreover, while it has been shown that, in some crosses of black males with orange females, a large percentage of patroclinous males may be expected (ANNA R. WHITING 1925), none are produced in crosses between stock 3 and stock 11. The latter stock is closely related to stock 14 of the present experiment.

mentioned generations shows how their potential defectiveness increased:

Generation	Average defect (M_n)	Percent defective
F_3	$2.61 \pm .08$	69.94
F_5	$4.08 \pm .17$	82.40
F_7	$3.62 \pm .11$	78.20
F_9	$4.45 \pm .14$	83.98
F_{11}	$4.21 \pm .14$	84.78

These averages are in harmony with the general upward trend of stock 14 at the time.

The heterozygous females

The females of the successive sexual generations should show the combined effect of the increasing defectiveness of stock 14, and the accumulation of the factors l , m , n , due to the process of breeding up.

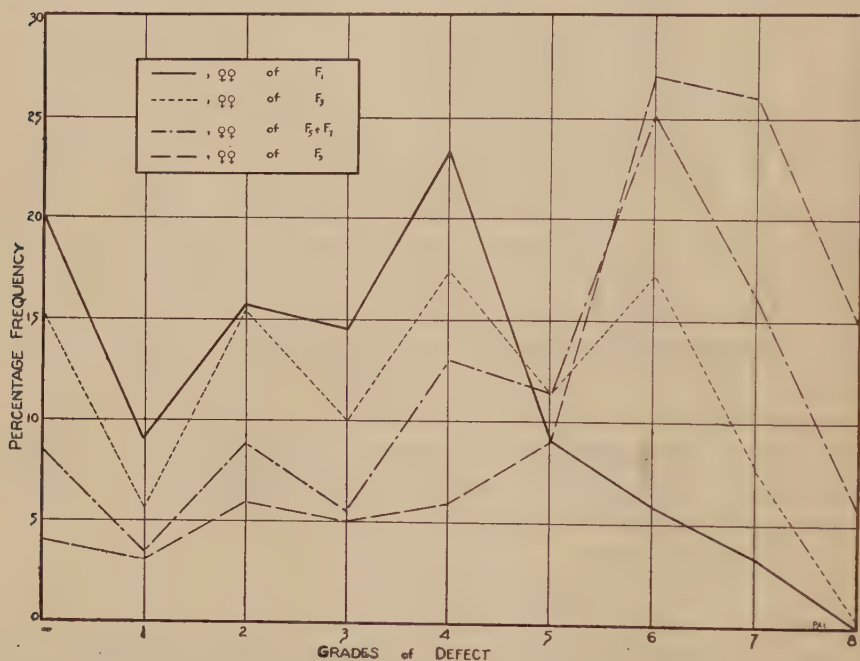


DIAGRAM 5.—Distribution with respect to grade of defect, derived from the cross, stock 14 $\times$ stock 3.

Table 4 shows the distribution of female wasps in these generations, and diagram 5 depicts it graphically (except that F_{11} is omitted). In F_1 all the females are heterozygous for all the factors involved; there is a distinct mode at 0 and another at 4; these modes suit the formula $DdLlMnNn$ very well. In the successive generations the mode at 4 gradu-

TABLE 4

Stock 14 × stock 3. Summary of data brought out by means of the special method employed.

GENERATION	PARENTS	OFFSPRING													
		Kind	Grade of defect										Total	Averages	
			0	1	2	3	4	5	6	7	8	Mean defect		Percent defective	
F ₁	Stock-14 ♀ ♀ × stock-3 ♂ ♂	♂ ♂ (stock 3)	6	6	12	7	45	21	45	39	21	202	5.18 ± .10	97.03	
		♀ ♀ heterozygous	35	17	29	27	43	17	11	6	0	185	2.81 ± .10	81.08	
F ₂	Virgin F ₁ ♀ ♀	♂ ♂ orange black	162	26	45	22	58	25	44	36	41	459	3.01 ± .09	64.71	
			130	22	44	26	58	19	53	56	55	463	3.60 ± .07	71.93	
			292	48	89	48	116	44	97	92	96	922	3.30 ± .07	68.33	
F ₃	Stock-14 ♀ ♀ × F ₂ ♂ ♂	♂ ♂ (stock 14)	135	37	72	42	59	31	43	24	6	449	2.61 ± .08	69.94	
		♀ ♀ heterozygous	45	17	46	30	52	34	51	23	1	299	3.52 ± .09	84.95	
F ₄	Virgin F ₃ ♀ ♀	♂ ♂ orange black	84	18	26	15	19	8	44	48	63	325	4.10 ± .12	74.16	
			49	7	21	15	23	8	42	43	75	283	4.87 ± .13	82.69	
			133	25	47	30	42	16	86	91	138	608	4.49 ± .11	78.13	
F ₅	Stock-14 ♀ ♀ × F ₃ ♂ ♂	♂ ♂ (stock 14)	19	5	10	7	19	4	20	13	11	108	4.08 ± .17	82.40	
		♀ ♀ heterozygous	6	1	13	8	17	8	19	1	1	74	3.89 ± .13	91.90	
F ₆	Virgin F ₅ ♀ ♀	♂ ♂ orange black	76	7	26	12	17	2	31	31	99	301	4.53 ± .12	74.67	
			63	14	22	12	16	13	28	35	97	300	4.71 ± .13	79.00	
			139	21	48	24	33	15	59	66	196	601	4.62 ± .09	76.87	
F ₇	Stock-14 ♀ ♀ × F ₆ ♂ ♂	♂ ♂ (stock 14)	46	19	21	12	18	19	40	28	8	211	3.62 ± .11	78.20	
		♀ ♀ heterozygous	14	7	8	11	14	19	41	37	13	164	4.97 ± .12	91.47	
F ₈	Virgin F ₇ ♀ ♀	♂ ♂ orange black	89	14	32	16	22	14	42	31	144	404	4.71 ± .11	77.97	
			82	16	39	10	21	11	54	42	150	425	4.90 ± .08	80.71	
			171	30	71	26	43	25	96	73	294	829	4.81 ± .08	79.38	
F ₉	Stock-14 ♀ ♀ × F ₈ ♂ ♂	♂ ♂ (stock 14)	29	10	18	6	16	7	41	35	19	181	4.45 ± .14	83.98	
		♀ ♀ heterozygous	4	3	6	5	6	9	27	26	15	101	5.57 ± .23	96.00	
F ₁₀	Virgin F ₉ ♀ ♀	♂ ♂ orange black	29	7	10	14	12	5	11	17	63	168	4.94 ± .16	82.74	
			21	2	8	5	16	7	25	20	81	185	6.16 ± .10	88.65	
			50	9	18	19	28	12	36	37	144	353	5.54 ± .10	85.84	
F ₁₁	Stock-14 ♀ ♀ × F ₁₀ ♂ ♂	♂ ♂ (stock 14)	23	7	13	15	18	19	36	16	14	151	4.21 ± .14	84.78	
		♀ ♀ heterozygous	26	4	11	9	11	11	32	21	16	141	4.39 ± .16	81.56	
F ₁₂	Virgin F ₁₁ ♀ ♀	♂ ♂ orange black	23	1	7	3	2	3	7	9	28	83	4.60 ± .25	72.29	
			17	3	5	2	4	2	9	6	40	88	5.20 ± .25	80.69	
			40	4	12	5	6	5	16	15	68	171	4.90 ± .17	76.49	

ally disappears and is replaced by a growing one at 6 (WHITING 1924, pp. 33-35). Apparently the cultures that produced F_{11} were not typical. In order to secure an adequate number of high-defective virgin females for the final crosses, ten cultures had been set; after the desired females had been obtained these cultures were discontinued. There were 141 females, and the tabulations showed that the progenies of three of the matings were abnormally low. Whatever the reason for this, the result was disastrous on tables and diagrams; F_{11} falls far below expectation.

The parthenogenetic males

The curve of the heterozygous females is quite different from that of their haploid male offspring. The distribution of the latter may be studied from table 4 and diagram 6, though the latter was designed primarily to demonstrate linkage of orange eye with low defect. Compare diagrams 1 and 3. These males are D or d with theoretically in F_2 an equal distribution of l , m , n , and their allelomorphs. The curve of F_2 corresponds quite well with what would be expected if the curve for males of stock 3, line B, were superimposed on that of stock 14 in its early unselected state. A comparison of the distribution of such a combination with the actual condition in F_2 is striking:

Grade.....	0	1	2	3	4	5	6	7	8
Expected.....	21.6	7.9	10.1	5.0	11.3	7.3	13.3	11.6	11.3
Observed.....	31.6	5.2	9.6	5.2	12.5	4.8	10.0	10.0	10.4

There are more types and fewer high-defectives than expected, but the discrepancy is accounted for by the redistribution of l , m , n , and their normal allelomorphs, if we assume that the latter are more effective in combination with d than the former. The progress in successive generations is clear-cut, as shown by the following summary:

Generation	Average defect (Mn)	Percent defective
F_2	$3.30 \pm .07$	68.33
F_4	$4.49 \pm .11$	78.13
F_6	$4.62 \pm .09$	76.87
F_8	$4.81 \pm .08$	79.38
F_{10}	$5.54 \pm .10$	85.84
F_{12}	$4.90 \pm .17$	76.49

The drop in the twelfth generation may be accounted for by the accidental use of wasps somatically high but with the factor D . Inspection of the records reveals that all the males of generation 12 were descended from one stock-14 female used as a parent in generation 11 (culture C137), and that the constitution of this female was low as measured by the

average of her sons (Mn 3.32). Compare what was said above about the heterozygous females of F_{11} .

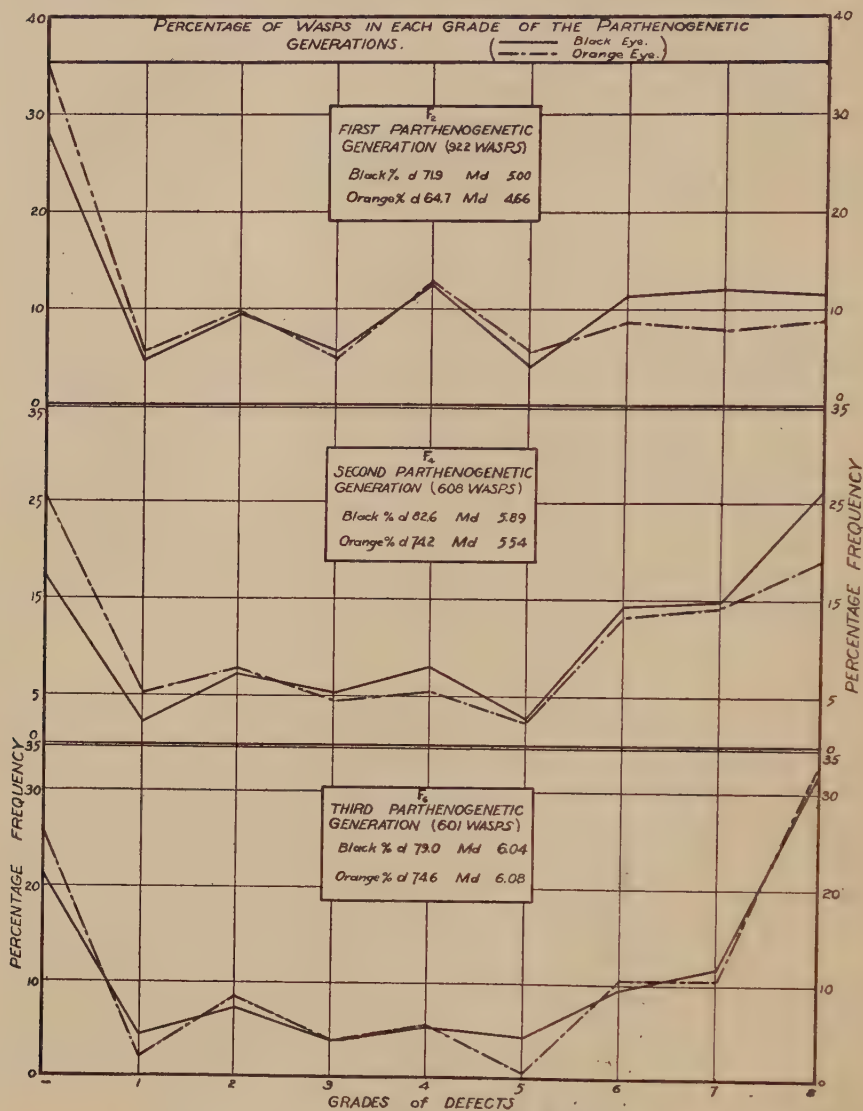


DIAGRAM 6a.—Showing the shift in distribution from the low grades to the higher in the succeeding parthenogenetic generations, and the persistent higher defectiveness of the black-eyed wasps.

Significant in the distribution curve is the depression at grade 5 which is found in all generations, and is fully equalled only by the drop at grade 1 in F_{10} . Apparently the D sons fall largely to the left of this mode and

the *d* sons to the right (WHITING 1924, p. 35). That the number of minor factors for defect are progressively accumulating in the *d* wasps is evidenced by the fact that, whereas grade 8 rises distinctly in each generation

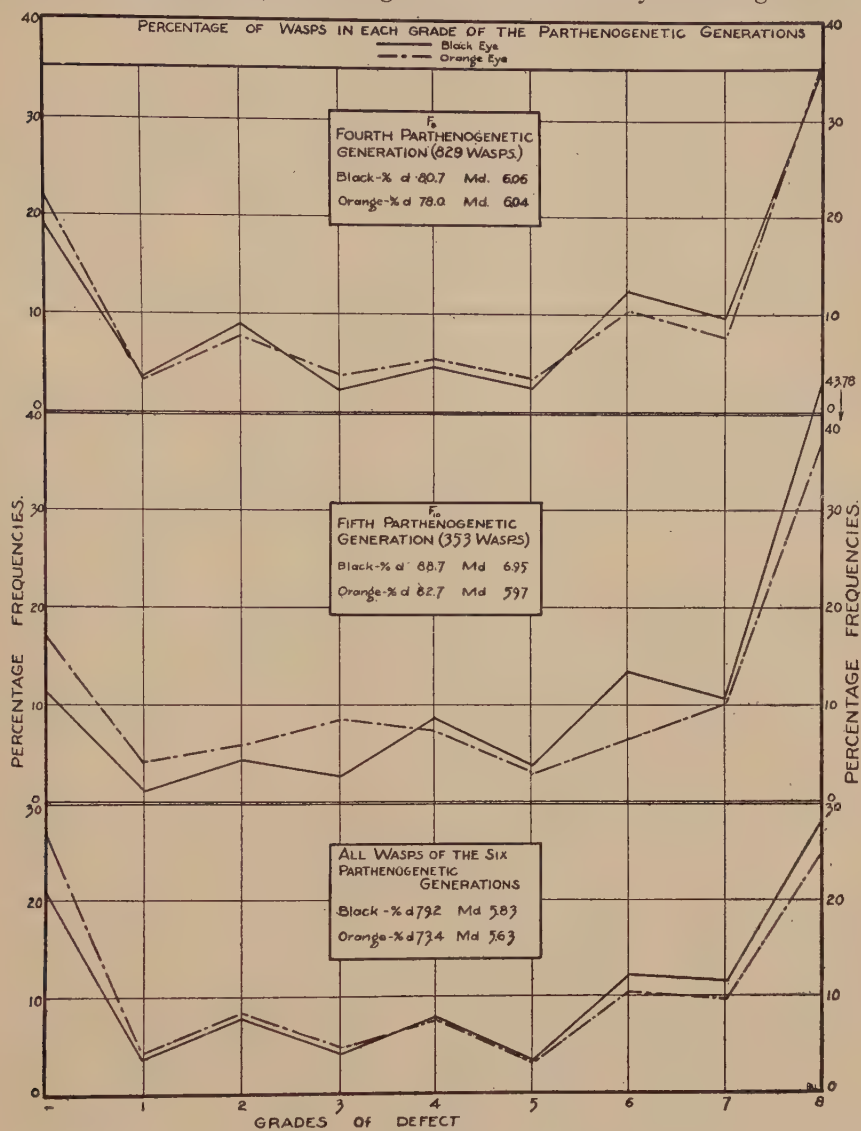


DIAGRAM 6b.—A continuation of diagram 6a.

(except as explained for F_{12}), grades 6 and 7 show no progress. In the *d* wasps without the minor factors (stock 3) the mode for the males was at 7 (compare diagram 1).

It seems clear from all this that if those wasps that do not possess the factor *d* could be eliminated, the remaining ones would show a higher-defective condition than stock 3. This is accomplished in the next experiment.

CROSS OF THE HETEROZYGOUS FEMALES AND PARTHENOGENETIC MALES

Grade-8 virgin females were now isolated from F₁₁ and mated with grade-8 males from F₁₀ and F₁₂. Seven such crosses were made, but five of the resulting lines were discarded in the course of the experiment. Only the last two lines are here discussed. Compare table 5 and diagram 7.

TABLE 5

Progenies of crosses between parthenogenetic males from generation 12 and heterozygous females from generation 11. All selected high-defectives.

Line 6. Leading to stock 16

GENERATION	SEX	GRADE OF DEFECT									TOTAL
		0	1	2	3	4	5	6	7	8	
First generation.....	♂ ♂	1	0	0	2	1	1	2	3	7	17
	♀ ♀	3	1	0	0	0	3	1	10	11	29
Second generation (No. 191).....	♂ ♂	0	0	0	1	2	1	3	16	63	86
	♀ ♀	0	0	0	0	0	0	1	3	26	30
Third generation (progeny of No. 191).....	♂ ♂	0	0	1	2	1	4	6	32	83	129
	♀ ♀	1	2	0	1	2	3	13	46	125	193

Line 7. Leading to stock 15

GENERATION	SEX	GRADE OF DEFECT									TOTAL
		0	1	2	3	4	5	6	7	8	
First generation.....	♂ ♂	0	0	0	1	2	0	2	3	6	14
	♀ ♀	0	0	0	0	1	1	4	8	20	35
Second generation (No. 181).....	♂ ♂	0	0	0	0	0	0	1	9	43	53
	♀ ♀	0	0	0	0	0	0	0	3	34	37
Third generation (progeny of No. 181).....	♂ ♂	0	1	0	0	3	3	16	90	313	426
	♀ ♀	1	0	1	1	1	8	10	72	278	372

Line 6

Culture T172 produced 17 males and 29 females. One male and three females were type, but the latter were dwarf, indicating that there was

insufficient food. The average of all the defectives was 7.00. From this culture two grade-8 females mated with their brothers produced widely different averages. T189 gave the following:

	<i>Number</i>	<i>Mn</i>	<i>Percent d</i>
Males.....	37	5.19	78.38
Females.....	43	6.76	87.68

T191 averaged much higher:

	<i>Number</i>	<i>Mn</i>	<i>Percent d</i>
Males.....	86	7.61	100.00
Females.....	30	7.83	100.00

T189 was discarded. From T191 five cultures were made that gave fairly uniform results. Their averages follow:

	<i>Number</i>	<i>Mn</i>	<i>Percent d</i>
Males.....	129	7.41	100.00
Females.....	193	7.40	99.48

The one type female was a dwarf and should be eliminated, thus bringing the percentage of defectives up to 100. These wasps are all black-eyed and are preserved as stock 16.

Line 7

Culture T173 gave 14 males and 34 females, all defective, the males averaging 6.75, the females 7.23. A mating from this culture (T181) gave offspring as follows:

	<i>Number</i>	<i>Mn</i>	<i>Percent d</i>
Males.....	53	7.79	100.00
Females.....	37	7.92	100.00

Fifteen grade-8 females from this culture were bred and gave quite uniform averages. They are as follows (diagram 7):

	<i>Number</i>	<i>Mn</i>	<i>Percent d</i>
Males.....	426	7.64	100.00
Females.....	372	7.62	99.73

As in line 6 there is one type female that should be disregarded because she is a dwarf. The wasps of this line are orange-eyed.

The progeny of T181 has been retained as the basis of a new stock, number 15.

In comparing this stock with the original line B of stock 3, it should be noted that in this final strain the difference between males and females is negligible; hence, comparison should be between males. The difference in favor of stock 15 (for males) is: $Mn, 1.61 \pm .036$; percent d, $2.53 \pm .17$.

Equally significant is the change in the distribution curve (compare diagrams 1 and 7). The mode in stock 15 is at grade 8 and the curve disappears almost completely at grade 5. This probably represents a combination of all, or nearly all, the factors for defect.

BACKCROSS WITH STOCK 14

Four backcrosses of type males from the parthenogenetic generations with low-grade females of stock 14 were made, partly to serve as a control

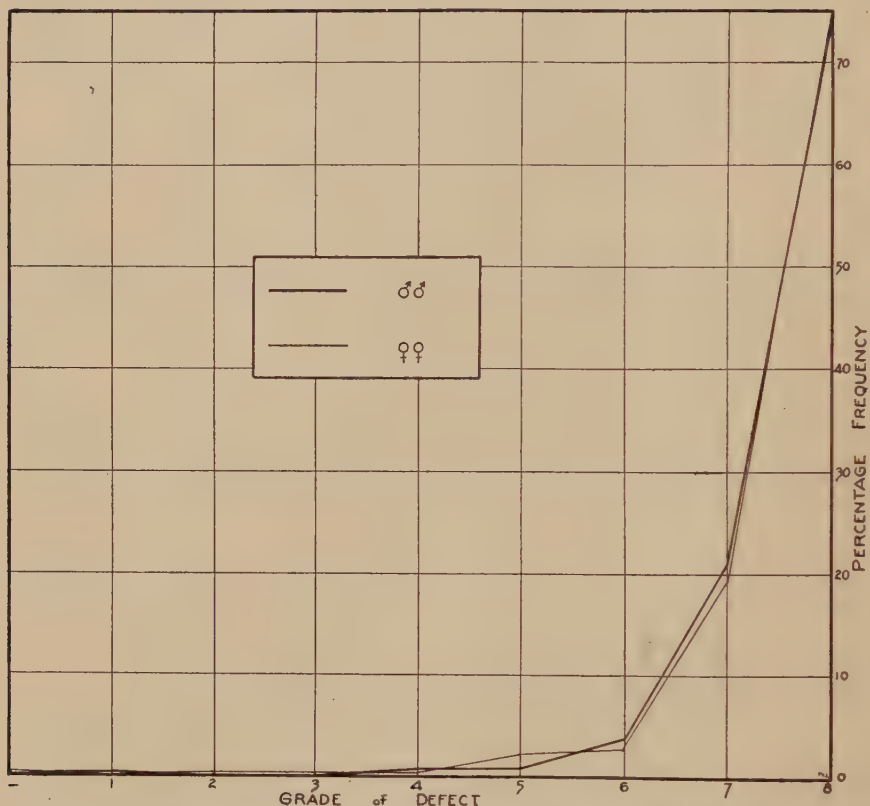


DIAGRAM 7.—Distribution with respect to grade of defect, of progeny resulting from cross between F_{11} heterozygous females and F_{12} parthenogenetic males.

to the high-defective cultures, and also to discover the genetic constitution of the type individuals of the parthenogenetic generations. Large numbers were bred from two cultures that differed conspicuously. In the second generation F_{141} produced 73.96 percent defectives and F_{171} gave 58.59 percent defectives. The Mn was 3.39 and 2.41, respectively. In the third generation, presumably as the result of selection, the averages dropped

much lower, as shown in table 6, and the difference between the two lines remained equally striking. In seeking an explanation of this difference the parents of the two lines were investigated. The female used in F171 comes from a line of stock 14 that is considerably lower than that from which the F141 female was taken. Besides, there had been a conspicuous drop in the parthenogenetic males of F_{12} below those of F_{10} , and the male parent of F171 was taken from the former, while F141 was derived from the latter.

TABLE 6

Progenies of backcrosses between low-grade parthenogenetic males from generations 10 or 12 and low-grade females from stock 14.

GENERATION	SEX	GRADE OF DEFECT									TOTAL
		0	1	2	3	4	5	6	7	8	
First generation. . .	♂ ♂	17	10	7	12	11	4	2	4	0	67
	♀ ♀	18	5	10	8	6	8	4	1	0	60
Second generation. .	♂ ♂	128	48	55	28	26	14	16	3	0	318
	♀ ♀	71	21	36	29	15	16	21	2	0	211
Third generation from F141.	♂ ♂	135	38	47	46	34	20	9	5	0	334
	♀ ♀	65	15	35	26	19	13	5	0	0	178
Third generation from F171.	♂ ♂	287	64	75	36	42	17	8	3	0	532
	♀ ♀	214	55	57	31	23	8	4	1	0	393

		From F141		From F171
Averages of third generation	Mean defect	♂ ♂	1.78	1.21
		♀ ♀	1.88	1.08
	Percent defective	♂ ♂	59.59	46.06
		♀ ♀	63.49	45.55

The wasps from this backcross average much lower than the wasps of the original stock 14. When we consider that the females of stock 14 used in these cultures were taken from stock 14 after it had shown the effect of selection (diagrams 3 and 4) the result is somewhat anomalous. However, there seems to have been a sudden drop in at least one line of stock 14 as suggested by the low averages of F_{11} and F_{12} , and as seems almost demonstrated by an analysis of the males resulting from the first generation of the backcross. These males are, of course, pure stock 14 except as affected by patrocliny which in this case is probably a negligible factor (P. W. WHITING 1924, p. 40; A. R. WHITING 1925). Their curve as

plotted from table 6 is very similar to the first cultures of stock 14 (diagram 8, $F_1 \sigma\sigma$).

It is noteworthy that of 2093 wasps examined from this backcross, not one was defective grade 8.

LINKAGE OF ORANGE WITH DEFECT

In the cross of stock 14 by stock 3 the factor *o* came in with the factor for high defect, *d*, and *O* came in with the factors for low defect, *l*, *m*, *n*. The males of the parthenogenetic generations were tabulated to show any

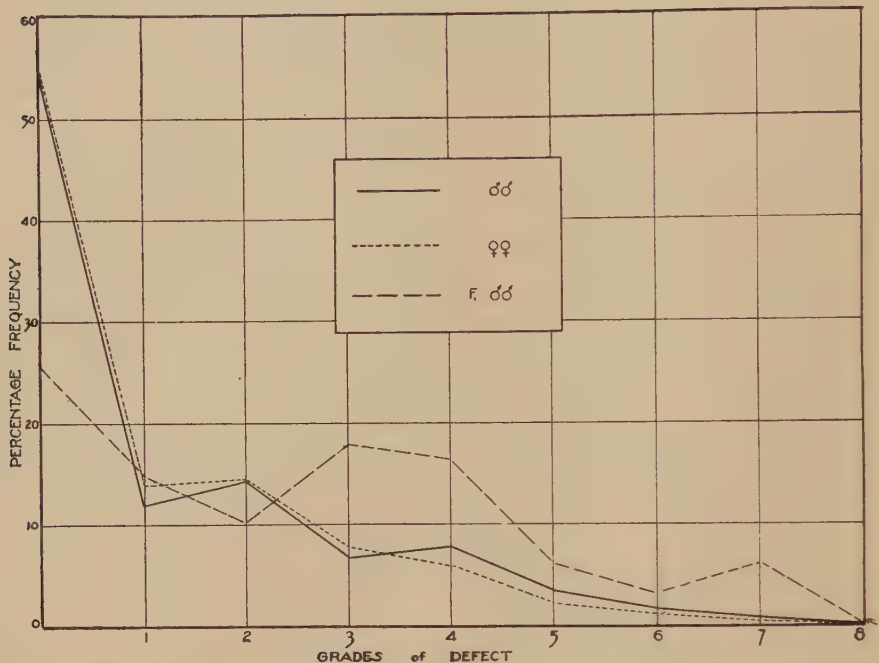


DIAGRAM 8.—Progeny of backcross with stock 14, showing the percentage of wasps in each grade.

relation between eye color and defective condition. The numbers and distribution of defectives in each eye-color group are shown in table 4, and the facts are illustrated graphically in diagram 6. Of 3484 wasps examined, 1740 were orange-eyed and 1744 black-eyed, indicating that there is no significant difference in viability. But the ratios and averages of defectives differ conspicuously and consistently in all generations. The black-eyed are more defective. This means that one or more of the factors *l*, *m*, *n*, are linked with eye color. This linkage has already been pointed out by WHITING (1924, p. 45).

There is no conclusive evidence of crossing over. In F_6 and F_8 the differences are smaller than in the other generations, but there is no reversal of the difference except in the average of defectives (Md) of F_6 . This is probably accidental. In F_6 there were 301 orange-eyed wasps, 225 of which were defective, and 300 black-eyed wasps, 237 of which were defective; but the 225 defective orange averaged slightly higher than the 237 black. A very few of the 76 orange that were somatically free from defect might have lowered the Md if they had become defective grade 1. In this connection it may be well to emphasize that these wasps are all genetically defective and hence type individuals do not represent a class by themselves; they are merely an extreme variation from the mean, caused, as the other variations, by external or internal environmental conditions, and they are classed together in one group only because there is no external indication of how far this tendency toward extreme variation goes (P. W. WHITING 1924, p. 49). If the curve were complete it would probably taper off to the left. In a word, type individuals represent an accumulation of extreme variants that cannot be accurately classified. For this reason the Mn should be considered more significant than the Md; it takes into account the extreme variant called type, whereas the Md does not include type specimens at all.

LINKAGE RELATIONS OF SOOTY CHEST

Sooty chest is a highly variable character present in stock 14. Wasps of stock 3 raised at 30° C have a clear yellow chest, whereas in stock 14 the color varies from jet black to yellow. For purposes of study three grades are distinguished: (a) the type color, yellow, labeled $s-$; (b) intermediate conditions, s_1 ; and (c) pure black, s_2 . Variation is affected by environment during development in a manner similar to that of vein defect, that is, low temperature and insufficient food tend to produce more sooty chest.

All wasps of the parthenogenetic generations F_4 to F_{12} were examined for chest color and the results tabulated. It was found that there is a positive correlation between black eye and sooty chest, which, though not large, is so constant that it must be significant. The following percentages are based on 1281 wasps in each group, all male, and of course bred under identical conditions. The black-eyed wasps examined have an average of $81.34 \pm .74$ percent sooty chest, and the orange-eyed wasps $77.53 \pm .79$ percent. The difference is 3.81 ± 1.08 percent. While the probable error is somewhat large, the following table shows that the ratios of these percentages remained fairly constant during the five generations examined.

Generation	Percentage of sooty chest		Ratio of orange to black
	Orange eye	Black eye	
F ₄	81.23	83.40	.954
F ₆	80.40	84.00	.952
F ₈	74.75	81.41	.913
F ₁₀	73.21	75.67	.966
F ₁₂	74.70	77.27	.952

Since orange eye is not a variable character the correlation cannot be accounted for by any theory of concomitant variation, as might possibly be done in the case of sooty chest and defective vein, both of which are variable characters. The above data indicate one of two things: either there is linkage between one of the factors for sooty chest and the factor for eye color, or black eye is itself a factor for sooty.

The correlation between chest color and vein defect is quite marked. Table 7 summarizes the data, based on the same wasps as above.

TABLE 7

GRADE	NUMBER OF WASPS				PERCENT SOOTY CHEST
	Yellow		Sooty S ₂	Total	
	S —	S ₁			
0.....	6	41	486	533	91.19±0.82
1.....	1	5	83	89	93.26±1.80
2.....	3	17	176	196	89.80±1.46
3.....	0	6	98	104	94.23±1.54
4.....	9	15	128	152	84.22±2.00
5.....	6	6	61	73	83.56±2.91
6.....	5	37	250	292	85.62±1.38
7.....	11	54	218	283	77.03±1.65
8.....	55	250	535	840	63.69±1.12
Totals.....	96	431	2135	2562	79.43±1.04

There is an increase of sooty chest from 63.69 ± 1.12 percent in wasps of grade 8 to 92.24 ± .59 percent in wasps of grade 3 to type. The largest percent of sooty chest is at grade 3, but this mode is probably not significant, its difference from type being only 3.04 ± 1.73 percent.

Since sooty chest was introduced into these wasps in combination with factors for low-grade defect, the correlation here found is all the more significant. The conclusion seems justified that there is a genetic linkage between some of the factors for defect and those for sooty chest.

SUMMARY

1. Breeding from individuals selected for opposite extremes of the variable character, defective venation, in a well-established stock of

Habrobracon juglandis, through nineteen generations in one direction and twenty-two generations in the other, has produced no significant difference in the progeny of the two lines.

2. A similar selection experiment, less rigid in method, in another stock that had not previously been inbred, resulted in an immediate change in the direction of selection, the mean defect after ten generations being increased nearly three-fold.

3. By breeding one defective stock to another, the various factors for defect can be concentrated, and they have a cumulative effect.

4. The haploid males of this insect furnish a unique and convenient method for the analysis of heterozygous females; a method that has special value in the case of factors that govern a variable character.

5. Application of the principles named under 3 and 4 has resulted in the creation of two new stocks (Nos. 15 and 16) showing defect in practically all individuals when the usual environmental conditions are maintained, and throwing an average defect of 7.64 as against 5.81 for the highest average previously attained. Expressed in percentages this is an increase from 77.2 percent to 95.5 percent.

6. The factor for orange eye is linked with one or more of the minor factors for defect.

7. There is a significant correlation between black eye color and sooty chest.

8. Amount of defect is negatively correlated with sooty chest, suggesting linkage of some of the factors for defect and those for sooty chest.

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